

# A REVIEW AND NEW CLASSIFICATION OF THE BRACHIOPOD ORDER PRODUCTIDA

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**ABSTRACT.** The authors discuss the large and diverse Upper Palaeozoic strophomenide (*sensu lato*) group of brachiopods, the Productida, the problems inherent in previous classifications and present a new classification with diagnoses down to subfamily and tribe levels. In describing productides it is useful to differentiate between the main corpus (new term) cavity and peripheral cavities. Study of the ways in which the two valves grew leads to more precise identification of the visceral and trail regions of the shell. New data on early productides, from the lower to mid Devonian, has allowed the group to be studied in its complete stratigraphical range, as well as its wide morphological diversity, and has led to the recognition of numerous lineages and homeomorphic relationships. The new classification presented builds on these lineages phyletically and differs markedly from previous classifications in which some similar taxa, now recognized as having different origins, were grouped together. We diagnose two new tribes, the Krotoviini and the Kozlowskiini.

THE order Productida, as here discussed, is made up of the true productidines, strophalosiidines and oldhaminioids, but follows Muir-Wood and Cooper (1960) and Lazarev (1990), for example, in excluding chonetoids, which some researchers (Sarycheva (ed.) 1960) included. This group has long been considered difficult to classify. Davidson (1859) wrote 'the determination and arrangement of British Carboniferous species of *Productus* and *Chonetes* has demanded a lengthened examination, for much confusion still existed among the synonyms,' while Girty (1908) considered that 'as a whole the group has shown unusual plasticity, developing not only widely different types, all referable to the same genus [*Productus*], but also abundant intermediate stages between what one would suppose to be wholly distinct species. In consequence, specific discrimination among '*Producti*' has always been a difficult matter, and authors have shown wide differences of opinion as to where the limits of species should be drawn.' Similarly, Yanishevsky (1918) wrote that the 'group represents perhaps the most complex group of brachiopods, for which it is impractical at the present time to give a clear picture of the generic relationships.' The few genera described in 1918 had risen to 167 by 1960 when Muir-Wood and Cooper published their beautifully illustrated monograph on the Productoidea, in which they wrote that 'No classification...yet produced has proved satisfactory.' With the proliferation of genera since 1960 their classification, used also by Williams *et al.* (1965), has also proved to be unworkable because taxonomic discrimination is not always clear and lineages were seldom considered. Here we offer a classification based on a mix of external and internal characters which persisted during unbroken lineages. We hope this classification can be used to determine taxa, even when less than perfectly preserved.

Lazarev has studied productides since 1974, with contributions on ontogeny (1981), and especially morphological evolution (1985, 1986) and systematics of Devonian taxa of the Strophalosiidina (1989) and Productidina (1990). For over 25 years Brunton has retained an interest in productides, particularly their varied growth features and palaeoecology (e.g. 1965, 1966, 1972, 1982, 1985, and, with Mundy 1988). Grant has dealt with Permian faunas over many years, especially the environmental settings of all productides (e.g. Grant 1963, 1966, 1968, 1972, 1976; Cooper and Grant 1972, 1975).

With the revision of the brachiopod part of the *Treatise on invertebrate paleontology* now under way, we have combined our interests to review classifications of this difficult group and present a

TABLE 1. List of characters, their type (ordered or unordered) and states used in the production of the matrix (Table 2) from which the cladogram (Text-fig. 1) was constructed.

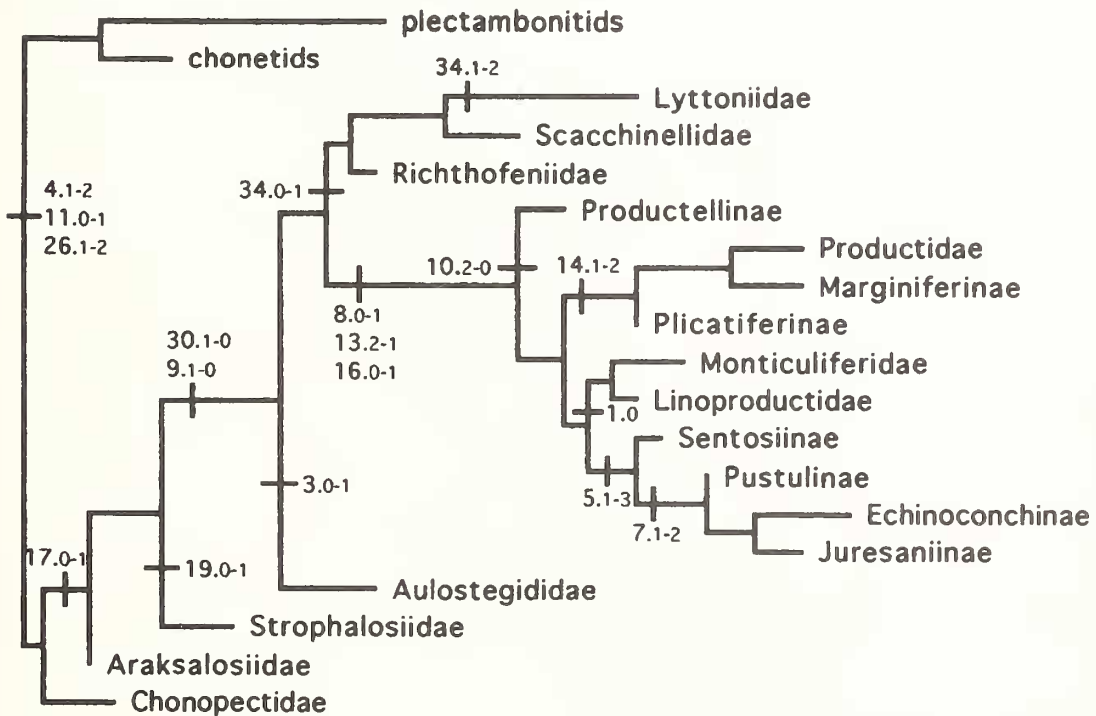
Character	Type	State
1. Fine ribbing	U	Present (0); absent (1)
2. Costae	U	Costate (0); non-costate/smooth (1)
3. Acquisition of costae	U	None (0); anteriorly (1); fully (2)
4. Spines	O	None (0); hinge only (1); general (2); lost (3)
5. Spine distribution	U	None (0); ventral only (1); mostly ventral (2); ventral plus dorsal (3); lost (4)
6. Spine types	U	None (0); thin (1); mostly thick (2); few symmetrical (3); attachment (4)
7. Spine bands	U	None (0); not banded (1); banded (2); bands only anteriorly (3)
8. Interareas	O	Present (0); absent (1)
9. Teeth also post Famennian	O	No (0); yes (1)
10. Corpus depth	U	Shallow (0); moderate (1); deep (2)
11. Aderidia	O	Present (0); absent (1)
12. Dorsal lamellae	U	Absent (0); present (1)
13. Trails	U	Absent (0); long (1); bordering structures (2)
14. Rugae	U	Absent (0); present (1); strong (2)
15. Posterior reticulation	U	Absent (0); present (1)
16. Cardinal process	O	Directed posteroventrally (0); directed posterodorsally (1)
17. Cicatrix	U	Absent (0); present (1)
18. Spine-base swellings	U	Absent (0); present (1)
19. Spines bidirectional	U	No (0); yes (1)
20. Corpus width	U	Small < 20 mm (0); medium/large (1); gigantic > 101 mm (2)
21. Ventral hinge spines	U	Present (0); absent (1)
22. Lateral ridges	U	Absent (0); present (1)
23. Cardinal ridges	U	Absent (0); present (1)
24. Marginal structures	U	Absent (0); present (1)
25. Alveolus	U	Absent (0); present (1)
26. Shell structure	O	Fibrous (0); 'mixed' (1); laminar (2)
27. Cardinal process	U	Not bilobed (0); weakly bilobed (1); strongly bilobed (2)
28. Dorsal platforms	U	Absent (0); present (1)
29. Brachial ridges	O	Absent (0); present (1); weak (2)
30. Brachial ridges area	U	Confined posteriorly (0); widespread + anteriorly (1)
31. Dorsal median septum	U	Absent (0); variable (1); strong (2)
32. Ventral median septum	U	Absent (0); variable (1); strong (2)
33. Dental plates	O	Commonly present (0); absent (1)
34. Profile	U	Concavo-convex (0); conical (1); flat (2)

new one which we hope can be used in the newly revised *Treatise*. We stress that the classification here presented is in a state of development and may not be exactly as will be published in the future brachiopod *Treatise*. We believe, however, that the structure is now sufficiently developed that later changes may be peripheral. The 167 genera described by Muir-Wood and Cooper (1960) has increased to about 500 nominal genera now being considered within the group.

An important weakness in previous classifications was that most of the information was derived from Carboniferous and Permian genera, as few of the Devonian productoid genera were then known and these provided scant evidence for the origin and early evolution of the group. This problem was tackled by Lazarev (1989, 1990) and we now have established productide genera in the

Lower Devonian which can be seen to have their origin in the chonetids (Brunton 1965, 1972; Johnson 1976). More importantly for the classification, increased knowledge of productide evolution in the Devonian allows their morphological trends to be established and these are fundamental to the systematics of the complete group. By the end of the Devonian the major trends of morphological diversity were established, with the separation of the strophalosiidines and three major groups of productidines. Through the Carboniferous and Permian periods recombinations of this diversity, together with some innovations, produced a wealth of genera within lineages, some of which display parallelism in aspects of their morphology. Previously these morphological similarities led to combinations of only distantly related genera in a classification based more on grades of evolution than on clades. Our emphasis is to develop monophyletic lineages of genera from their earliest ancestors and, in this way, to separate genera with superficial similarities into what we believe are more biologically realistic taxa or clades.

In order to provide a more objective assessment of the developing classification 34 characters, well displayed in genera throughout the Productida and belonging to 17 of our proposed family groups, plus 2 outgroups, were subjected to an introductory analysis on a PAUP 3 program. All characters were equally weighted and have from two to four states, and those marked with an 'O' in Table 1 were ordered. The plectambonitoids and chonetidines were specified as rooted outgroups, respectively being distantly related and widely considered (e.g. Johnson 1976) as ancestral to productides, as well as having geologically older representatives. The heuristic search retained a single most parsimonious (non-consensus) tree of length 103 (Text-fig. 1). Despite its provisional



TEXT-FIG. 1. Cladogram tree of 17 family-group taxa within the Productida constructed from 34 characters listed in Table 1. No character was weighted, but those marked 'O' in Table 1 were ordered. The plectambonitids and chonetids were specified rooted outgroups. Synapomorphies are identified by their character number and change of state (see text for further details).

and unrefined nature, the tree clearly separates the Productidina as a monophyletic clade with rather poorly discriminated strophalosiidines forming a more diffuse paraphyletic grouping in which the unusual morphology of the Lytoniidae, Scacchinellidae and Richthofeniidae causes them to be almost separated. The Productidina divides into three groups, the Productoidea (Productellinae to Plicatiferinae), Linoproductoidea (Monticuliferidae and Linoproductidae) and Echinoconchoidea (Sentosiinae to Juresaniinae) (Table 2). The Productellinae, which includes the stem group for all

TABLE 2. Matrix of characters (Table 1) distributed amongst the named taxa.

plectambonitids	10200000100000000-010?010010-1000
chonetids	010111101000000000000101110102210
Lytoniidae	1103400100100000100110000211110012
Richthofeniidae	1102241002102000100110001210201011
Aulostegidae	1112241001102100100110111220101010
Scacchinellidae	11022410021000001001?0100221100211
Strophalosiidae	1102221011102000101000100210112010
Chonopectidae	1102111010100100000000001210211010
Araksalosiidae	1102211010100000100000101210111010
Productellinae	1112111100101001000111001210102010
Productidae	1022131102111211000101010221102010
Monticuliferidae	0102111100101101010100000210102010
Linoproductidae	0102111102101101000101010210102010
Sentosiinae	1102313100101101000101000210102010
Pustulinae	1102313102101101010100100210102010
Echinoconchinae	1102312102101201000100110221102010
Juresaniinae	1102313102101101010101111220102010
Marginiferinae	1022231102111111000011010210102010
Plicatiferinae	1102131102101201000111010210102010

productoids, is placed topologically as sister group to all other productidines although, in our classification, it is grouped within the Productoidea (see 7-9 on Text-fig. 3).

A survey of historical studies of productides and full discussions on the methods, character states, origins and evolution of the Productidina is to be found in Lazarev (1990).

Since 1990 we have concentrated mostly upon the large and diverse groups of productoids derived from what were called the Productellidae by Lazarev (1990, fig. 11). Two of us (SSL and CHCB) have in preparation a revision of this stem group family for the Productoidea in which genera are regrouped into subfamilies and tribes according to our view of their evolutionary history. The summary of diagnoses in the appendix herein includes our current views on the Productellidae.

#### METHODS AND CHARACTERS USED IN THE CLASSIFICATION

An important characteristic of the productide shell is its body cavity depth. However, this feature also influences other internal and external features which we need to be able to describe accurately. We find ambiguity in the literature amongst terms describing shell surfaces, such as the 'visceral disc' and 'trails'. There is no uniformity in their use or precision as to what is meant, so we present a system of terms enabling the whole productide shell to be described accurately in a way which is also meaningful to its growth. Productides with a deep shell cavity normally have dorsal valves which are geniculated against the ventral valve. Commonly, growth of the dorsal valve, relative to the ventral valve, was slow. Thus at about half the fully adult curved length of ventral valves, the dorsal valve had virtually stopped growing anteriorly, only adding to the length of its trail. It was at about this half-full-growth stage when the ventral valve commonly changed its growth direction slightly or conspicuously (the geniculation point: Text-fig. 2G), and in many species their surface

ornamentation also changed. This is the stage at which trails first started to develop and from which the two valves grew more or less parallel to each other. Lazarev (1981), dealing with general ontogeny in productoids, and Timms and Brunton (1990), dealing more specifically with growth rates and geniculation in some productoids, suggested that sexual maturity initiated these growth changes. While dorsal valves did not add much to body length (other than for a series of external trails and internal diaphragms in some species), ventral valves continued to grow beyond the 'geniculation point', but commonly with a changed growth spiral so as to become more tightly coiled and with the developing trail more dorsally directed. This pattern of ventral valve growth continued throughout the rest of the brachiopod's life. Growth of both valve trails was along parallel curves and commonly followed a radius of curvature centred on the hinge axis. In some species, during earlier stages of ontogeny, the complete dorsal valve rotated dorsally to some extent and, in so doing, increased the body cavity depth (Brunton 1985). The fully adult ventral valve interior was marked in many species by a ridge onto which the dorsal valve rested when the shell was closed. There is, however, uncertainty in the literature as to what constitutes the trail; whether only the adult regions of shell formed the functional trails, or also the region of the ventral valve which had been a functional trail during earlier stages of growth and by adulthood formed part of the main body of the productide?

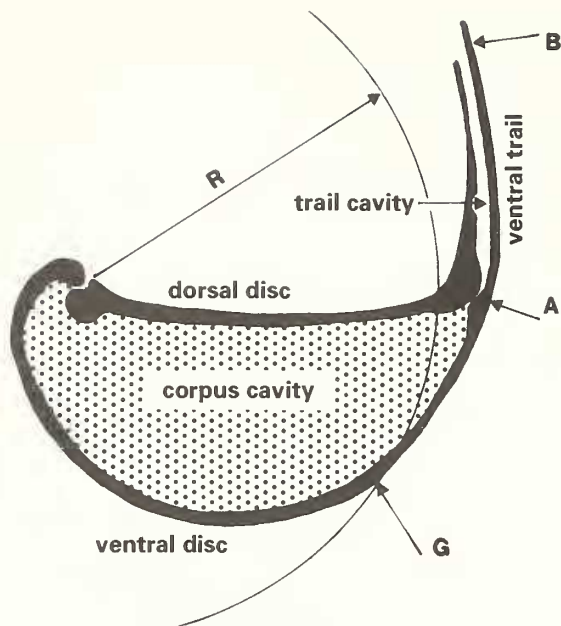
It is not uncommon for the main body region of the shell to be preserved while the ears and trails are lost, and although it may be possible to recognize a point from where ventral trails started to grow and where ornament changes, only the body region can be fully described. Text-figure 2 illustrates a sectional view through a typical deep-bodied productide to which we have added terms we use in describing parts of the shell. We are unable to use the word 'body' in our specific meaning, as it is defined by Williams (1965) to mean the posterior coelomic region containing the main brachiopod organs, other than the lophophore. The terms take into account changes during ontogeny and many are equally useful in describing shallow-bodied productides, i.e. those with a shallow 'corpus' cavity. Indeed, we believe that a clear distinction between 'corpus' and 'peripheral' areas could be equally useful in describing other brachiopod groups, such as some strophomenides or athyrididines. It should be noted, however, that in shallow productides, as there is no strong geniculation in the dorsal valve, the disc lengths of both valves are more similar than in deep shells and their valves grew more closely parallel to each other during ontogeny. In addition there is no universal 'R' value amongst productides; it varies interspecifically, and to a small extent intraspecifically. For instance in a genus like *Overtonia*, each ventral ruga and dorsal lamella was associated with a 'R' value as they grew (Brunton 1985). In *Diaphragmus*, with its preserved series of dorsal trails, the 'R' value is taken at the first-formed dorsal trail and then corresponds with the ventral geniculation point; the subsequent trails correspond to the ventral protrail.

We introduce the following terms (Text-fig. 2):

**Corpus.** That part of the shell comprising the two valves enclosing the posterior body (visceral) cavity plus the mantle cavity (which housed the lophophore in life), but excluding the shelly extensions forming ears and trails. Thus the term can be used to describe surface areas of the shell and the cavity enclosed, as defined above.

**Peripheral cavities.** Cavities peripheral to the corpus cavity, narrowly enclosed between marginal regions of the valves in areas such as the ears or trails in productides or between frills, flanges etc. in athyrididines.

**Protrail** (Latin *pro*, before, and trail). Region of the ventral adult corpus, anterior to the point of geniculation (Text-fig. 2G), which functioned as a trail during earlier growth stages and over which ornamentation commonly changed, resembling that on the true ventral trail. The anterior margin of the protrail can only be defined in adult shells, as the position at which the dorsal valve rested against the ventral inner surface when the shell was closed. In some species this position was marked by internal shell thickening or by less obvious changes in the ornamentation of the inner surface



TEXT-FIG. 2. Stylized section of a closed adult productidine, with deep corpus cavity and trails, showing the terminology used. R – the radius of curvature, centred on the hinge axis, limiting the dorsal and ventral disc lengths, and point G – the geniculation point on the ventral valve at which a major or minor change in growth direction commonly took place; A – the position of rest of the adult dorsal disc against the ventral valve interior; B – the margins of the adult trails. The shell corpus is the dorsal and ventral discs plus the protrail (G–A). These surfaces enclose the corpus cavity (shaded). Totrail – G–B.

(Text-fig. 2A). In terms of growth, the protrail corresponds to the dorsal valve region of marginal ridges or diaphragms, where present.

Totrail (Latin *totus*, complete, and trail). The total length of ventral trail development from the point of geniculation to the valve margin. It is the protrail plus the true ventral trail (Text-fig. 2G–B).

### The characters

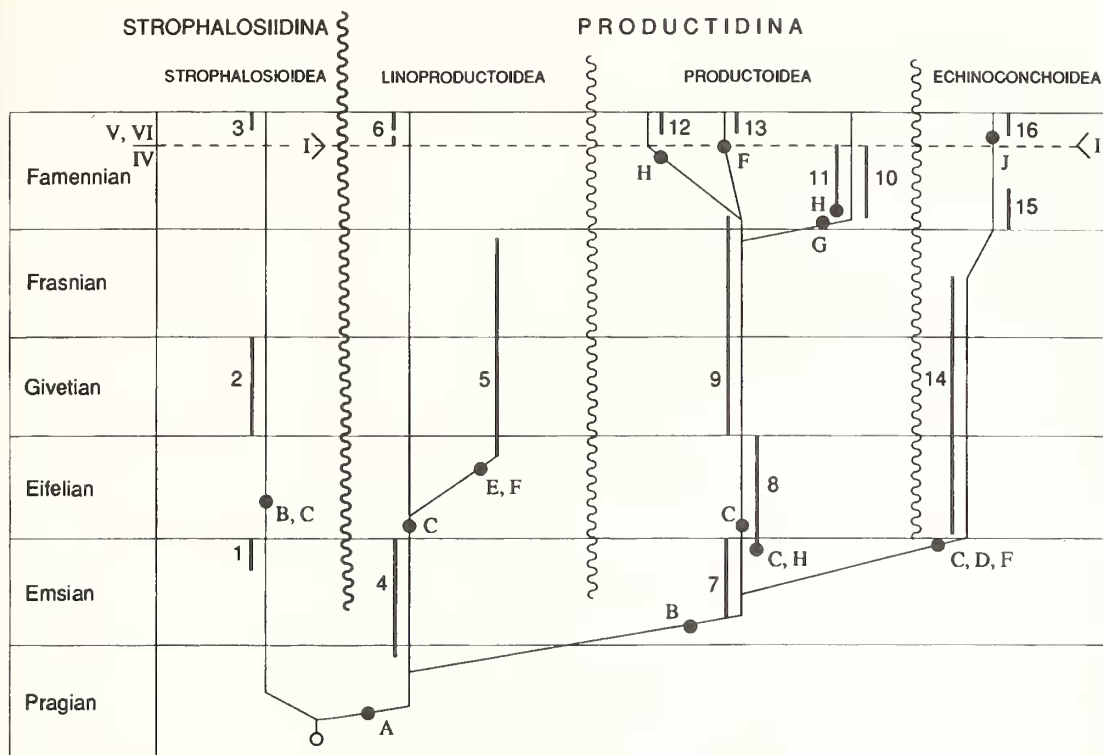
We have attempted to provide a classification which is evolutionary, that is by following lineages, but we recognize that reversals in character trends have occurred.

A process recognized in this classification is that some characters first appeared late in ontogeny, but during evolution appeared increasingly early in the ontogeny of later individuals. Thus, in some productidines, ribbing, for example, may appear first towards the adult anterior valve margins and progressively, through time, has 'spread' posteriorly to cover most or all of the valve or shell. In this way a shell with a smooth umbo, but which is otherwise ribbed, can be identified probably as having evolved from non-ribbed stock.

Emphasis on the importance of some characters has been developed through experience and is used in the classification suggested here. Characters of the greatest importance are those which display ontogenetic and phylogenetic stability; those which arose early in ontogeny and remained throughout the life of the individual, and which also persisted through a long period of time. On the other hand characters that appeared in one or more lineages but lasted only briefly in species of few genera, are of little use in classification above generic level.

The most characteristic feature separating the Productida from their chonetid ancestors is the spread of spines from the hinge line of chonetids to covering the ventral valves of the Productida.

The first apomorphy within the Productida, separating the Strophalosiidina from the Productidina, is the loss of a true interarea in the latter. By a true interarea, we mean growth at the posterior margin which developed at a high angle from the rest of the ventral valve, and in so doing increased valve separation posteriorly. This is in contrast to valve thickening along the posterior margin of some productidines which produced what appears externally like an interarea, but instead

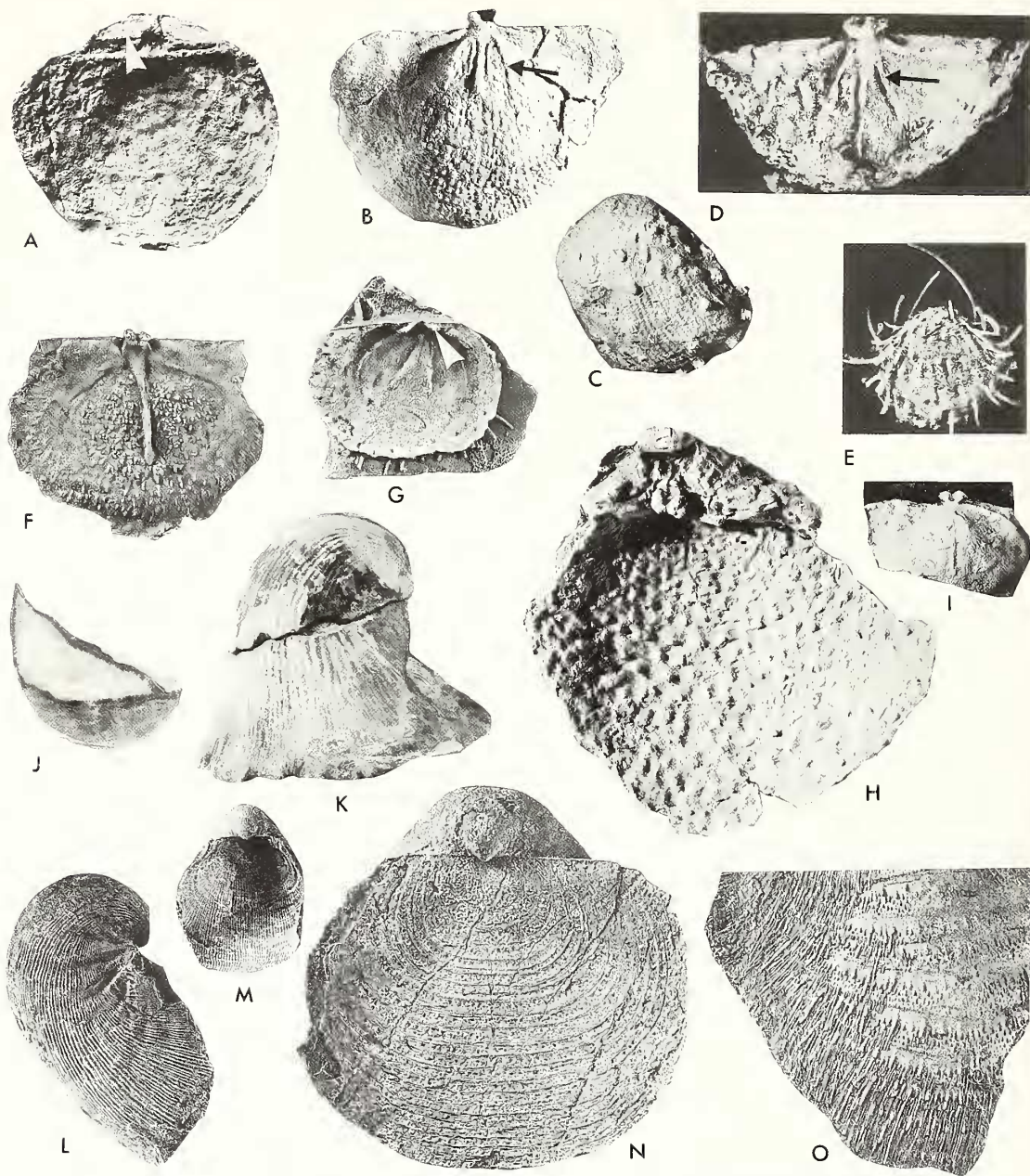


TEXT-FIG. 3. The major morphological changes in Devonian Productida giving rise to the Strophalosiidina and Productidina. Character changes are identified by letters A to J, and the earliest genus in each superfamily, plus others of significance, are numbered 1-16. Characters: A - Loss of interareas. B - Loss of fine chonetid-like ribbing. C - Loss of anderidia. D - Development of dorsal spines (not important in the Strophalosioidea). E - Development of serial dorsal lamellae. F - Development of marginal structures. G - Development of deep corpus cavity. H - Introduction of anterior ribbing. I - Loss of toothed articulation in the Productidina. J - First differentiation of spines into bands. Taxa: 0 - 'Chonetid' ancestor from which the spread of spines over the ventral valve gave rise to the Productida. 1 - *Ralia*. 2 - *Devonalosia*. 3 - *Acanthatia*. 4 - *Eoproductella*. 5 - *Devonoproductus*. 6 - *Ovatia*. 7 - *Chattertonia*. 8 - *Spinulicosta*. 9 - *Productella*. 10 - *Ardiviscus*. 11 - *Nigerinoplica*. 12 - *Dorsirugatia*. 13 - *Rugauris*. 14 - *Caucasiproductus*. 15 - *Praewaagenoconcha*. 16 - *Laminatia*.

is a ginglymus with layers of shell material subparallel to the external valve surface. It is noteworthy that anderidia, inherited from the chonetids, which when fully developed probably aided the support of the body wall, are found in species attributed to both the strophalosiidines and productidines (Text-fig. 4B, D) in the Pragian and Emsian (Text-fig. 3, character C), indicating a common ancestry for the Productida.

Text-figure 3 shows the early to mid Devonian evolution of the Productida and the next levels of morphological changes important in their classification. Of fundamental importance in the early stages of evolution, and in dividing the productidines into three basic components are:

1. Preservation of fine ribbing on the valves, inherited from the chonetids, which characterizes the linoproductoids (Text-fig. 4C).
2. Loss of this fine ribbing, producing relatively smooth shells, the productoids (Text-fig. 4E), which in the middle and upper Devonian developed strong costation anteriorly.



TEXT-FIG. 4. A selection of Devonian and early Carboniferous genera from the Strophalosoidea (A, F-G), Linoproductoidea (B-C, L-M), Productoidea (D-E, J-K), and Echinoconchoidea (H-I, N-O) showing important features of morphology. ANU: Australian National University, Canberra; B or BB: The Natural History Museum, London; PI: Palaeontological Institute, Moscow; USNM: National Museum of Natural History, Washington, DC, USA. A, *Ralia*; PI 4217/2; Gobi-Altai, Mongolia; Lower Devonian, Emsian; dorsal view; note the interarea and fine radial ribbing;  $\times 3$ . B-C, *Eoproductella*; PI 4114/120 and 4114/121; Tadzhikistan, central Asia; Lower Devonian, Pragian to Emsian; note the anderidia (arrowed) on the dorsal interior and fine ribbing on the ventral exterior;  $\times 4$  and  $\times 3$ . D-E, *Chattertonia*; ANU 18951.1 and 18951.j; New South Wales, Australia; Lower Devonian, Emsian; note the anderidia (arrowed);  $\times 3.5$  and  $\times 2$ . F-G, *Devonalsosia*;



3. Appearance of fine, but closely arranged spines also on dorsal valves introduced the echinoconchoids (Text-fig. 4H).

We accord superfamily status to these three groups, being the first level of divisions within the Productidina.

Next in importance is a suite of characters helping to discriminate between families and subfamilies, usually when they appeared for the first time:

I. Depth of the corpus cavity. A useful measure of this is the length of the dorsal valve divided by the maximum depth of the cavity. Those shells with a ratio of three or less are considered as deep (e.g. Text-fig. 4J).

Ia. Shells with shallow corpus cavities are characterized by a concavo-convex lateral profile and trails which are commonly simple and without dorsal geniculation.

Ib. A deep cavity results primarily from a tight spiral curve of the ventral valve, especially of the tottrail, together with geniculation of the dorsal valve anteriorly. This is an important characteristic within the productidines, appearing first in the lower Famennian.

II. The development of marginal ridges at the internal edges of the corpus. These ridges developed progressively through ontogeny at or near the margins of the valves; they separate the corpus cavity from peripheral areas such as ears and trails. Marginal ridges include lateral ridges, ear baffles and subperipheral ridges near the lateral and anterior margins; we include also diaphragms and cinctures. The degree of development of marginal ridges differs among and between groups and in some was associated with the growth of trails. Cardinal ridges, at the hinge, did not function as cavity separations. The relationship between cardinal or lateral ridges and ear baffles can be important, as is the degree of development of these ridges, especially those which served to isolate the corpus cavity posterolaterally.

III. The development of marginal ridges in Carboniferous and Permian taxa may be associated with a series of anteriorly positioned dorsal trails.

IV. The loss of ventral spines at or near the hinge line.

Other characters of varying taxonomic importance and which may recur throughout productide evolution are:

a. The loss of toothed articulation in the Productidina in the Famennian, but its common retention in the Strophalosiidina (Text-fig. 4G).

b. The appearance, early in ontogeny, of a series of trails on dorsal valves.

c. The appearance (in species younger than late Devonian) of ribbing on the disc regions.

d. The development of a strong concentric ornament (lamellae or rugae) over the disc areas. In association with radial ribbing this concentric ornament may produce a reticulate ornamentation posteriorly.

e. Spines became differentiated according to size within concentric bands (Text-fig. 4N-O).

f. Spines became restricted to a few (commonly no more than eight) long and thick halteroid spines, symmetrically placed. These are in addition to small juvenile spines near the hinge or on the ventral umbo, which may be difficult to distinguish.

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USNM 123439c and 123432j; Ontario, Canada; mid Devonian, Givetian; note the posteroventrally projecting cardinal process, interarea and teeth (arrowed);  $\times 3$ . H-1, *Caucasiproductus*; PI 4127/187 and 4127/101; Transcaucasia, Armenia; mid Devonian, Eifelian to Frasnian; note spine bases covering the dorsal valve and long lateral ridges;  $\times 3$  and  $\times 1$ . J-K, *Productus*; BB19691; Derbyshire, England; Lower Carboniferous, Asbian; note the deep corpus cavity (seen in section J showing geopetal structure) and long spreading trail;  $\times 1$ . L-M, *Ovatia*; USNM 124101 and 124103; Oklahoma, USA; Lower Carboniferous, Chesterian; note the fine radial ribbing and lack of dorsal spines;  $\times 1$ . N-O, *Echinoconchus*; BB13629 and B24012; Yorkshire and North Wales; Lower Carboniferous, Viséan; dorsal view (N); part of ventral valve viewed anterolaterally (O); note spine bands on both valves, deep corpus cavity and short trails,  $\times 1$  and  $\times 2$ .

- g. The dorsal adductor scars evolved to a more anterior position, so that the scar plus its trace left a gap between them and the hinge line, which may have accommodated a posterior segment of the mantle cavity.
- h. The development of bordering structures at the valve margins during late stages of ontogeny; these including flanges, gutters, carination and tube-like growths of ventral valves.
- i. The juvenile presence of buttress plates anterior to the cardinal process, retained or submerged by secondary shell during ontogeny.
- j. The development of dorsal muscle platforms raised above cavities. These may be outwardly curving plates from their median fusion with the valve floor, or ones rooted laterally and curved medianly.

Other morphological features, such as a relatively narrow hinge, differentiation of the myophore scars and their dividing ridges on the cardinal process, gigantism (a width of more than 100 mm at the corpus), monticules or the development of strong spines near the dorsal hinge line, are commonly restricted to genera within small subfamilies.

In the Strophalosiidina some of the above characters assume different importance and there are additional features of importance. These include the degree of development of the interareas; the presence of a cicatrix; the development of spines which, on the same area of shell, grew in opposite directions; the loss or retention of toothed articulation; conical valve shape; cystose shell growth; a strong ventral median septum and the presence of a myocoelidium.

The Oldhamioida share a pseudopunctate shell with other productides and Liao (1983) reported the presence of rare ventral spines; an observation confirmed by one of use (REG). Another link, with at least some strophalosiidines, is the so-called dorsal valve, which has been shown to be mainly a ptychophous brachidium, with the actual 'valve' reduced to an articulatory process at the hinge (Termier and Termier 1949; Williams 1953; Grant 1972). An important feature amongst Carboniferous taxa is the symmetry of the muscle marks. Later forms are differentiated according to size (and numbers of lateral lobes), orientation of the lateral lobes, presence or absence of a 'hood', orientation of the ventral lateral septa and whether the shell's mode of attachment was by the beak only, by the posterior flap or by major parts of the ventral valve. The nature of the substrate bears upon the form of attachment.

#### POST-DEVONIAN EVOLUTION

By the late Famennian most of the main characteristics of the productidines had developed, as shown in Text-figure 3. Some characters were introduced and reintroduced among and within different evolutionary lineages during the Carboniferous and Permian. For instance, strong radial ribbing appears first in the mid Devonian in *Spinulicosta*, a productellid, on its anterior trail only. Then in the early Famennian, in *Nigerinoplica*, one of the first genera of the Leioproductinae with a deep corpus, ribbing appeared anteriorly but soon was present over much of the corpus. In many productoid groups this ribbing came to a climax, commonly covering the whole shell, by the late Tournaisian, and ribbing persisted through into the Permian. In other productoids there was another 'explosion' of ribbed genera starting in the Artinskian (early Permian). After the introduction of dorsal spines in the echinoconchoids, dorsal spines were introduced independently in several productoid families. Thus, in the early Carboniferous, dorsal spines appeared in examples of buxtoniins, overtoniins and some plicatiferins. In the Permian they reappeared in some species of the Marginiferinae, having been lost from the lineage in middle Carboniferous species. Within the linoproductoids a tubiform ventral valve developed in Carboniferous *Proboscidella* and Permian *Tubaria* and *Siphonosia*, yet all three were derived from different ancestors (indeed it might be argued that the last belongs in the aulostegoids on account of its deep corpus, rhizoid spines, small cicatrix and widely placed brachial impressions, but an interarea is lacking).

In each of the three productidine superfamilies there are two persistent groups; genera with a shallow corpus and those in which the cavity is deep. However, we recognize also that some taxa

within either of these major groups reverted, via intermediate depths, to the opposite condition. Within the Productidina as a whole there is a general trend towards deepness in the Permian, but some genera demonstrate exceptions to this and reverted to shallow cavities.

During Carboniferous and Permian times morphology changed drastically amongst the entire Productida, contributing to the wide diversity of taxa. Some of the most marked changes occurred amongst strophalosiidines. Hardgrounds and framework reef facies were rare in the Carboniferous but led to morphologies that were reflected in the more common reefs and bioherms of the Permian. The more widespread occurrence of species living on relatively soft sea floors led to a variety of patterns of supporting spines posteriorly and on the venter, and to protective spines at the valve margins throughout ontogeny or only at late stages of growth.

An important adaptation, probably leading to an enlarged lophophore and improved water-circulation system, was the deepening of the corpus cavity, first recognized in some lower Famennian leioproductins, then in echinoconchoids in the Tournaisian, and yet again in linoproductoids in the Viséan. Thereafter, families with deep or shallow corpus cavities are to be found in each of the superfamilies. A Permian adaptation, also interpreted as improving the water circulation system, was the introduction of the falafer brachidium, interpreted as supporting a folded ptychophe (Grant 1972), discovered in some small and cemented species which appear to have lived much as does the Recent *Thecidellina*. This change from the earlier productidine style of lophophore, probably a simple schizophe, took place in the mid Permian, although it is possible that an unsupported ptychophe may have developed in deep strophalosiids in the Upper Carboniferous and persisted well into the late Upper Permian.

In the Permian a few new features appeared in productides: large spines close to the dorsal hinge line in the Horrioniinae; strong bilobation of the shell outline in some of the Marginiferinae and Cooperininae; and monticules (external swellings commonly interrupting radial ribbing) in some of the Monticuliferinae. During the same period there was a diversification among strophalosiidines, with deeply conical ventral valves containing cystose tissues (Richthofenioida and Scacchinellidae) while a great array of bordering structures developed in the aulostegoids. Other morphologies, having their origins in the Carboniferous, were reworked and extended to create an amazing array of adaptive features, but the group died out by the close of the Permian.

The extinction of brachiopod faunas, particularly the Productida, late in the Permian took place somewhat earlier in North America than farther east in the Tethys region. The regressions led to shallowing and drying which affected the brachiopods living in relatively shallow water particularly severely, so that among productides only *Spinomarginifera* may have survived into the earliest Triassic (data from the Himalayas).

#### CLASSIFICATION AND DIAGNOSES

The classification is hierarchical, so characters are mentioned at their first appearance and may not be repeated at lower taxon levels. Thus, for instance, in the Linoproductoidea the lack of dorsal spines is almost universal and noted at the superfamily level; their presence being noted in the few relevant lower taxa. Thus several taxon levels have to be read to gain the most complete description of a subfamily or tribe. We use the taxon 'tribe' because, in the most diverse and long-ranging families of the Productoidea, we find insufficient taxa down to subfamilies alone in which to accommodate all definable groups within the lineages.

The diagnoses of lower taxa, especially tribes, should be viewed in their stratigraphical context in order to understand the patterns of changes which occurred within families and subfamilies.

Where we include mention of size we follow the convention: shells with a maximum corpus width of up to 20 mm are small; those between 21 and 50 mm are medium; those between 51 and 100 mm are large, and those 101 mm wide and over are gigantic.

In the description of lateral profiles the mention of an 'ideal spiral' means that the growth spiral is not distorted by any geniculation and, in consequence, the corpus cavity can be expected to be shallow.

## Order PRODUCTIDA

*Strophomenides sensu lato* with concavo-convex to planoconvex or conical corpus profiles, commonly with trails; spines on ventral valves or both, rarely reduced to hinge regions or absent from some; dental plates absent; cardinal process bilobate, commonly protruding, with varied recessed myophores; brachial markings commonly present; mantle canals rarely marked; shell substance with crested or sheet laminae and pseudopunctate with taleolae.

## Suborder PRODUCTIDINA Waagen, 1883

Productides lacking interareas or with ginglymus only; toothed articulation absent after latest Devonian; cardinal process directed posteriorly or posterodorsally, not ventrally; brachial ridges reniform, confined posteromedianly.

## Superfamily PRODUCTOIDEA Gray, 1840

Productidines with long trails, other than in early forms; ornamentation diverse, commonly costellate; spines may be absent from ventral hinge area, otherwise widely to closely spaced; dorsal spines commonly absent, when present not widely distributed.

## Family PRODUCTELLIDAE Schuchert, 1929

Shell small to medium sized; dorsal valve concave or, rarely, only slightly concave; ribbing absent from beak or totally; spines varied on ventral valve only and commonly absent from hinge region; corpus cavity shallow, rarely deep in Carboniferous or Permian taxa; teeth present or absent.

## Subfamily/Tribe

**Productellinae** Schuchert, 1929

Ribs rarely developed and then only anteriorly; spines evenly distributed over ventral valve only; corpus shallow; teeth present; lateral ridges and ear baffles lacking; cardinal process lobes divergent, V-shaped dorsally, with pit; dorsal adductor scars commonly non-dendritic.

**Productininae** Muir-Wood and Cooper, 1960

Productellids commonly ribbed, especially ventrally; few spines on ventral valve only, absent from hinge region; corpus cavity shallow, except in some *Paramarginiferini*.

**Productinini** Muir-Wood and Cooper, 1960. Ribbing on ventral valve and concentric lamellae prominent on dorsal valve; ventral profile an ideal spiral; no sulcus.

**Paramarginiferini** Lazarev, 1986. Radial ribbing and, in some, posteriorly reticulate; ventral profile distorted, ventral trail (when present) commonly becoming anteriorly nasute; ventral marginal ridges commonly developed.

**Chonetellini** Likharev, 1960. Outline subtriangular; ventral profile an ideal spiral; ribbing incipient or smooth; commonly nasute.

**Overtoniinae** Muir-Wood and Cooper, 1960

Ribs absent or rarely confined anteriorly on trails; spines scattered equally on both valves, but absent from ventral hinge; corpus depth varied.

**Avoniini** Sarycheva, 1960. Concentric ornament of broad irregular lamellose bands; ventral lateral profile an ideal spiral; corpus cavity shallow to moderate.

**Overtoniini** Muir-Wood and Cooper, 1960. Strong rounded rugae bearing spines; corpus cavity deep; dorsal adductor scars raised.

**Krotoviini** trib. nov. Concentric ornament weak or lacking; ventral profile an ideal spiral; shallow corpus cavity.

**Costispiniferini** Muir-Wood and Cooper, 1960. Concentric ornament weak; ribbing may be present on trails; ventral profile distorted, with shallow to deep corpus activity.

**Institiferini** Muir-Wood and Cooper, 1960. Minute to small shells with relatively deep corpus cavity, bearing concentric ornament and coarse ribbing on trails which are strongly deflected as flanges or gutters; spines on ventral corpus only.

**Marginiferinae** Stehli, 1954

Ribbing dominates concentric ornament (may be reduced in Permian); ventral profile commonly geniculate at start of protrail.

**New tribe** to be described formally elsewhere. Spines on both valves; ribs commonly start anteriorly on corpus with elongate spine bases posteriorly.

**Paucispiniferini** Muir-Wood and Cooper, 1960. Ventral spines only; always ribbed; corpus cavity may be deep.

**Marginiferini** Stehli, 1954. Ventral spines, rarely on both valves; always ribbed, but weakly; commonly with a series of dorsal trails and corpus cavity deep.

**Incisiini** Grant, 1976. Ventral spines only; ribbing absent; hinge narrow; lateral profile an open spiral.

**Plicatiferinae** Muir-Wood and Cooper, 1960

Shell geniculated, with ventral disc only gently convex; corpus cavity moderately shallow to, rarely, deep anteriorly; ribbing lacking, weak or only anteriorly on trails; concentric ornament normally strong, especially rugae; spines sparsely or densely distributed on ventral valves, commonly including near hinge, rarely on both valves.

**Rugaurini** Muir-Wood and Cooper, 1960. Corpus cavity shallow; trail absent or very short; no ribbing; dense spines covering ventral valve, rarely on dorsal valves anteriorly; teeth in oldest taxa; no ear baffles or submarginal ridges.

**Semicostellini** Nalivkin, 1979. Corpus cavity deep; costae on long trails; lateral and marginal ridges commonly well-developed, especially ventrally.

**Plicatiferini** Muir-Wood and Cooper, 1960. Corpus cavity moderately deep; trail long; ribbing absent or weak, only on trails; rugae, or lamellae, strongly developed on corpus; ear baffles in dorsal valve, rarely also in ventral valve.

**Levipustulini** Muir-Wood and Cooper, 1960. Geniculated dorsal valves with short trails; corpus cavity variable; rugae weak or lacking but spines numerous with pustulose bases, commonly on both valves, but lost dorsally in Permian; marginal structures and peripheral cavities reduced or absent.

**Levitusiini** Lazarev, 1985. Relatively large shells with long trails and moderate to deep corpus cavities; ribbing absent, but may be weak, fine radial striations; rugae weak; spines weak and sparsely developed, a row anterior to ears and commonly a ventral median row on weak ridge; weak cardinal ridges; no marginal ridges.

**Yakovleviini** Waterhouse, 1975 [= *Inflatiinae* Sarycheva, 1977]. Commonly medium-sized with thick-shelled ventral valve and moderately deep corpus cavity, becoming shallow in younger genera; ribbing on trails and all but posterior regions of corpus, with 4–6 thick ventral spines; common trend to reduce ear cavities and extend anterior peripheral cavity.

Family **PRODUCTIDAE** Gray, 1840

Commonly deep corpus, rarely moderate or shallow, but then with inflated ventral corpus; spine row(s) near hinge; teeth only in oldest genera.

**Leioproductinae** Muir-Wood and Cooper, 1960

Ribbing commonly absent or weak, never at beak; dorsal spines commonly absent; corpus cavity deep; teeth absent in all but oldest genera.

**Leioproductinae** Muir-Wood and Cooper, 1960. Small to medium-sized; ribbing absent, but commonly with ventral medium weak fold; ventral spines sparse, dorsal spines absent; teeth in early genera.

**Semiproductini** McKellar, 1970. Medium size, with deep corpus cavity and trails; elongate spine bases arranged quincuncially on ventral disc, spines extending onto trail; ribs originate anteriorly on discs and always occur on trails; lateral ridges commonly short, no marginal structures; teeth in early genera.

**Horridoniini** Muir-Wood and Cooper, 1960. Medium or commonly large, thick-walled valves; ribs weak or absent; 1-3 rows of halteroid spines on ventral ears and, rarely, one row near dorsal hinge; rarely other dorsal spines; marginal structures commonly absent.

**Tyloplectini** Termier and Termier, 1970. Ribbed, other than at beak; additional striae dorsally; ventral spines large near hinge and on flanks; probably absent dorsally.

#### **Dictyoclostinae** Stehli, 1954

Medium to large size; trails long, simple; ribbing complete with reticulation posteriorly; ventral spines commonly stout halteroid; dorsal spines absent; dorsal adductor scars positioned posteriorly, close to hinge line; marginal structures absent or weak.

#### **Productinae** Gray, 1840

Small to medium size; trails long, may have bordering structures; ribbing entire, reticulate posteriorly; spines commonly only on ventral valve; marginal structures well developed.

**Productini** Gray, 1840. Ribbing relatively fine; spines thin, numerous on ears; diaphragm associated with series of dorsal trails; dorsal adductor scars may be raised on platforms.

**Spyridiophorini** Muir-Wood and Cooper, 1960. Ribbing coarse, homogeneous anteriorly; spine row on each arched ear; no diaphragm or series of dorsal trails; dorsal adductor platforms well developed.

**Kozlowskiini** trib. nov. Spines variable, but may include few thick halteroid spines; zygidium may be present; marginal ridges associated with series of dorsal trails.

**Retariini** Muir-Wood and Cooper, 1960. Trail non-lamellose, may be tubiform; row of thick spines at base of ventral flank, sparse or absent from dorsal valves; dorsal adductor scars positioned relatively anteriorly.

#### **Buxtoniinae** Muir-Wood and Cooper, 1960

Size varied, but with corpus cavity deep; ribbing on trails and commonly on corpus; spines dense on both valves, but may be restricted anteriorly on dorsal valve; elongate cardinal process pit seldom absent; dorsal muscle scars separated from hinge region.

**Tolmatchoffiini** Sarycheva, 1963. Dorsal trail of varied length; ribbing covering both valves, other than in the early Tournaisian, when umbos smooth; rugae commonly absent, spines on ventral valve not uniformly distributed; cardinal process pit elongate.

**Buxtoniini** Muir-Wood and Cooper, 1960 [= Kochiproductini Lazarev, 1985]. Dorsal trail commonly short, bordering structures (flanges) sporadic; ribs cover both valves, other than in Tournaisian, when smooth posteriorly; rugae irregular, may dominate ribs; spines on ventral valve uniformly distributed, commonly from swollen bases; buttress plates and pit present, but variable.

### Superfamily ECHINOCONCHOIDEA Stehli, 1954

Productidines widest anterior to hinge, with corpus cavity deep in most families; trail commonly very short; spines covering both valves (including at hinge), commonly arranged in concentric bands, recumbent and forming dense mats; ribbing absent.

#### Family SENTOSIIDAE McKellar, 1970

Echinoconchoids having shallow corpus cavity; concentric bands and spine differentiation commonly absent.

#### **Caucasiproductinae** Lazarev, 1987

Sentosiids with teeth and sockets; ventral spines relatively thick, suberect; lateral ridges short, divergent anteriorly.

#### **Sentosiinae** McKellar, 1970

Sentosiids without teeth; spines thin, may have elongate bases.

**Sentosiini** McKellar, 1970. Concentric rugae or lamellae may be as bands anteriorly.

**Bagراسيini** Nalivkin, 1979. Elongate spine bases simulate ribs on both valves.

#### Family ECHINOCONCHIDAE Stehli, 1954

Corpus cavity deep; dorsal trail commonly short; spines thin, commonly in concentric bands, recumbent.

##### **Pustulinae** Waterhouse, 1981

Medium to large size; low rugae; spine base pustules may not be arranged in bands; buttress plates and cardinal process pit absent.

##### **Echinoconchinae** Stehli, 1954

Concentric bands well developed on both valves bearing spines differentiated in size; buttress plates and cardinal process pit absent.

**Echinoconchini** Stehli, 1954. Medium to large; concentric bands cuesta-like in profile, posterior part smooth and narrower than anteriorly where spines differentiated by size; one or two rows of thicker spines posteriorly, thinner rows anteriorly; dorsal adductor scars tend to become raised, crests curve laterally.

**Karavankinini** Ramovš, 1969. Small to medium size; high relief concentric bands, symmetrical in profile, tops bearing concentric rows of spines, distributed by size, separated by wider smooth bands; dorsal adductor scars raised, crests curved medianly, after Serpukhovian.

**Calliprotoniini** Lazarev, 1985. Medium size; concentric ornamentation of low, anteriorly somewhat lamellose bands covered by evenly distributed recumbent spines on each band, grading from large to small anteriorly; lateral ridges strongly developed and extending as submarginal ridges.

##### **Juresaniinae** Muir-Wood and Cooper, 1960

Concentric bands absent or confined anteriorly; spines may be differentiated by size anteriorly; cardinal process pit and buttress plates present in Carboniferous, but lost in Permian genera.

**Juresaniini** Muir-Wood and Cooper, 1960. Quincuncial pustules posteriorly; concentric bands of spines commonly on rest of valves; anteriorly rugose or lamellose.

**Waagenoconchini** Muir-Wood and Cooper, 1960. Corpus with small quincuncially arranged spines and dense mat of long peripheral spines; weak banding anteriorly; trails may be long.

#### Superfamily LINOPRODUCTOIDEA Stehli, 1954

Trail commonly long but simple; ribbing regular, entire and relatively fine, commonly delicately sinuose; ventral spines at hinge and diverse on rest of valve, never few, thick and symmetrical; dorsal valve without spines except grandaurispinins and some giganotoproductins.

#### Family MONTICULIFERIDAE Muir-Wood and Cooper, 1960

Linoproductoids with moderately shallow corpus cavity, rarely very shallow; rugae posterolaterally or irregularly widespread; spines on ventral valve, rarely restricted to hinge region; marginal structures normally absent.

##### **Eoproductellinae** Lazarev, 1987

Small or medium size; both valves or dorsal valve only with fine ribbing; spines on ventral valve only; teeth and sockets present.

##### **Auriculispinae** Waterhouse, 1986 [= Ovatiinae Lazarev, 1990]

Medium size with rounded to elongate outline; spines normally on ventral valve only, with clusters on ears; teeth and sockets absent; marginal structures commonly absent.

**Schrenkiellinae** Lazarev, 1986

Medium size to large, with flattened ventral disc; spines in row near hinge margin only; ribs separated by wider interspaces; rugae may be present.

**Compressopductinae** Jing and Hu, 1978

Small or medium size, elongate outline, hinge narrow; corpus cavity moderately shallow; valves thin-shelled with complete ribbing and rugae; spines rare, rhizoid; cardinal process a single median ridge (unifid), lateral ridges weak.

**Devonopductinae** Muir-Wood and Cooper, 1960

Moderately shallow corpus cavity; fine ribbing especially on ventral valve; dorsal valves with concentric lamellae as traces of series of trails; cardinal process pit absent; ear baffles in ventral valve and weak dorsal lateral ridges; weak submarginal ridge in dorsal valve with papillae.

**Gigantopductinae** Muir-Wood and Cooper, 1960

Gigantic, large or medium size, hinge at greatest width; corpus cavity very shallow; fully ribbed; spines on ventral valve, rarely also on dorsal valves; marginal structures commonly absent; cardinal process pit commonly present.

**Semiplanini** Sarycheva, 1960. Medium size to large, with very thin shell substance; ventral umbo strongly incurved; ribs of various widths; spines on both valves, some on ventral only; cardinal process bilobed or trifold, with median ridges poorly developed; no brachial cones.

**Gigantopductini** Muir-Wood and Cooper, 1960. Large or gigantic, thick-walled valves; ventral umbo not strongly incurved; commonly ribbed; spines commonly on ventral valve, only rarely on dorsal valve also; cardinal process trifold with median ridge well developed or sole element; brachial cones commonly distinct.

**Striatiferinae** Muir-Wood and Cooper, 1960

Shell large to medium; outline elongate or with tubiform trail, hinge narrow; spines on ventral valve only.

**Striatiferini** Muir-Wood and Cooper, 1960. Large, with very shallow corpus; trails simple; cardinal process of single ridge continuous with median septum.

**Proboscidellini** Muir-Wood and Cooper, 1960. Corpus cavity shallow; hinge narrower than maximum width; ventral trail long and forming tube, irregularly rugose; cardinal process bilobed, lateral and submarginal ridges present.

Family **LINOPRODUCTIDAE** Stehli, 1954

Linoproductoids with deep corpus cavity and distinct trails; commonly no dorsal spines.

**Linopductinae** Stehli, 1954

Linoproductids without marginal structures or dorsal spines.

**Grandaurispininae** Lazarev, 1986

Linoproductids with thin spines on dorsal corpus; marginal structures and series of trails absent.

**Siphonosiinae** Lazarev, 1986

Linoproductids with elongate outline and short tubiform ventral trail; hinge narrower than maximum width; spines rhizoid, on ventral valve only; marginal structures at borders of both valves [monotypic].



**Anidanthinae** Waterhouse, 1968

Linoproductids with well developed ears and marginal structures; concentric lamellae (series of trails) commonly on dorsal valve.

## Suborder STROPHALOSIIDINA Waagen, 1883.

Productides with interareas in ventral valve only or in both valves; commonly ventrally attached; profile includes conical shape; toothed articulation retained or lost; cardinal process directed ventrally or posteroventrally, never dorsally; brachial ridges commonly extending to disc margins.

## Superfamily STROPHALOSIOIDEA Schuchert, 1913

Interarea in ventral valve or both valves, commonly with cicatrix; corpus cavity shallow; teeth retained; brachial ridges spread widely.

## Family STROPHALOSIIDAE Schuchert, 1913

Outline rounded; strong rhizoid spines over ventral or both valves, may be bi-directional; planoconvex profile, but corpus cavity rather shallow; trails short or absent.

**Strophalosiinae** Schuchert, 1913

Spines on ventral valve only; concavoconvex profile.

**Dasyalosiinae** Brunton, 1966

Spines on both valves; dorsal valve commonly flat.

## Family CHONOPECTIDAE Muir-Wood and Cooper, 1960

Concavoconvex profile; shallow corpus cavity; cicatrix varied; trails short; fine radial ornament, rugae variable; hinge spines plus sparse and fine ventral corpus spines.

## Family ARAKSALOSIIDAE Lazarev, 1989

Interareas short; concavoconvex, shallow corpus cavity; radial ornamentation absent; cardinal process with pit, cardinal and marginal ridges commonly absent.

**Araksalosiinae** Lazarev, 1989

Cicatrix reduced; mat of spines on ventral valve, rarely dorsally, commonly with stout rows at ventral hinge; elongate spine bases may form incipient ribs.

**Donalosiinae** Lazarev, 1989

Cicatrix present, spines relatively thick; concentric ornament may be lamellose.

**Rhytialosiinae** Lazarev, 1989

Cicatrix present; undulose rugae prominent but discontinuous; spines dense on ventral valve, fewer on dorsal valve.

**Quadratiinae** Lazarev, 1989

Pseudodeltidium and chilidium commonly absent; concentric ornament well developed and regular; spines at low angle, rare on dorsal valve; marginal ridges present.

## Superfamily AULOSTEGOIDEA Muir-Wood and Cooper, 1960

Attached permanently by spines or direct cementation; ventral interarea present, dorsal interarea small or absent, no chilidium; trails commonly elaborated or conical in Permian, when corpus cavity became deep; teeth absent; brachial ridges may be restricted.

## Family AULOSTEGIDAE Muir-Wood and Cooper, 1960

Plano- to weakly concavo-convex profile; corpus moderately deep; ventral rhizoid spines prominent; cardinal process trifold or quadrid; adductor scars dendritic.

**Aulosteginae** Muir-Wood and Cooper, 1960

Elaborated trails; spines numerous, on both valves.

**Chonosteginae** Muir-Wood and Cooper, 1960

Small, with complex valve-like spinose trails at dorsal geniculation.

**Institellinae** Muir-Wood and Cooper, 1960

Corpus rugose to reticulate; trails commonly ribbed with bordering structures of flanges or gutters.

**Agelesiinae** Cooper and Grant, 1975

Corpus outline triangular; ventral interarea reduced; no dorsal spines.

**Rhamnariinae** Muir-Wood and Cooper, 1960

Interarea reduced or rudimentary; spines on both valves; cardinal process lobes strongly divided.

**Echinosteginae** Muir-Wood and Cooper, 1960

Dorsal spines absent; dorsal adductor scars on raised platforms.

## Family COOPERINIDAE Pajaud, 1968

Small; bilobate outline; cemented by large cicatrix, spines or both; hinge teeth and pseudodeltidium absent; dorsal interior with adductor platform and prominent brachial ridges.

**Cooperininae** Pajaud, 1968

Small-sized for family; ventral interarea and cicatrix surrounded by long rhizoid spines; dorsal muscle platforms short.

**Epiceliinae** Grant, 1972

Large for family; hinge narrow with small interarea; ventral spines restricted around cicatrix; brachial ridges multilobed.

## Family SCACCHINELLIDAE Likharev, 1928

Prominent ventral median septum and widely bilobed cardinal process.

**Scacchinellinae** Likharev, 1928

Ventral valve conical with transverse partitions apically; dorsal valve lid-like; deep corpus cavity.

**Tschernyschewiinae** Muir-Wood and Cooper, 1960

Concavo-convex profile; cicatrix common, plus support spines.

## Superfamily RICHTHOFENIOIDEA Waagen, 1885

Ventral valve conical or sphenoid, dorsal valve recessed below ventral margin; ventral valve attached by cicatrix, rhizoid spines, or by both; small interarea present in Upper Carboniferous genera, but lost from Gzhelian onwards.

## Family RICHTHOFENIIDAE Waagen, 1885

Conical; spines rhizoid; ventral myocoelidium.

## Family HERCOSIIDAE Cooper and Grant, 1975

Conical; spines rhizoid; ventral median septum.

## Family CYCLACANTHARIIDAE Cooper and Grant, 1975

Conical; spines rhizoid or absent; ventral muscle callosity.

**Cyclacanthariinae** Cooper and Grant, 1975

Conical; no spines in *Collumatus*.

**Teguliferininae** Muir-Wood and Cooper, 1960

Sphenoid (obliquely conical); spines rhizoid.

**Zalveriinae** Brunton, in press

Sphenoid to low conical; aspinose (other than tip of ventral beak), with shallow corpus cavity.

## Superfamily LYTTONIOIDEA Waagen, 1883

Shells attached by some part of ventral valve; dorsal valve reduced to small posterior region, the hinge and cardinal process; brachial apparatus supporting lophophore and functioning as partial 'dorsal valve' variable.

## Family POIKILOSAKIDAE Williams, 1953

Small shells attached umbonally or by entire ventral valve, often reflecting shape of substrate; ventral diductor scars asymmetrical; brachial apparatus consisting of two major lobes, each with 2–5 variously directed sublobes.

## Family LYTTONIIDAE Waagen, 1883

Ventral adductor scars medial; diductor scars symmetrical.

**Lyttoniinae** Waagen, 1883

Large; attached by ventral surface, beak, or posterior flap; brachial ridges multilobed.

**Rigbyellinae** Grant, subfam. nov.

Small; attached at beak; raised anteriorly; brachial lobes small, few, extending anteriorly.

**Permianellinae** He and Zhu, 1979

Small; attached at beak; bilobed outline; two proportionally large pustulose dorsal lobes directed anteriorly; ventral interior smooth.

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